

Stock–recruitment relationships for three major Alaskan crab stocks

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Abstract

Stock–recruitment (S–R) relationships have important implications for harvest strategies but are difficult to develop for crab stocks because crab lack retainable hard body parts to age them and lack of sufficient knowledge about complex crab reproductive biology also complicates estimating effective spawning biomass. To evaluate harvest strategies, we developed S–R relationships for three major crab stocks in Alaska: Bristol Bay red king crab, *Paralithodes camtschaticus*, Bristol Bay Tanner crab, *Chionoecetes bairdi* and eastern Bering Sea snow crab, *Chionoecetes opilio*. We used abundance and recruitment estimates from length-based models, based on growth data for recruitment age and estimated effective spawning biomass from male and female abundance, male fertilization capability, sex ratio, size and shell condition of males, molting period duration of the female population and duration of male attendance during mating. Results varied with species. For red king crab, weak recruitment was associated with extremely small spawning biomass and strong recruitment was associated with intermediate spawning biomass, suggesting possible density-dependent effects. However, the king crab recruitment trends were also consistent with patterns of decadal climate shifts. Results were equivocal and a general Ricker model fit the king crab data slightly better than an autocorrelated Ricker model. For Tanner crab, the autocorrelated Ricker model fit the data much better than the general model and most of the variability of Tanner crab recruitment can be explained by a cycle with a period of 13–14 years. For snow crab, the autocorrelated Ricker model generally fit the data much better than the general model and S–R observations formed a circular pattern. Despite the weak evidence for S–R relationships, harvest strategies must be precautionary to reduce the risk that crab stocks fall to levels so low that reproductive output is insufficient to produce large year classes when environmental conditions become favorable.

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1. Introduction

Estimating a stock–recruitment (S–R) relationship is an important part of developing an optimal harvest

strategy for a stock. An S–R relationship describes a probable recruitment level of progeny from a given reproductive stock size. If recruitment is not related to the corresponding reproductive stock size, then the optimal harvest strategy may be to harvest all animals that have reached their maximum economic value. However, because recruits are survivors from eggs that are spawned by the parent stock, it follows that depressed reproductive stocks will produce fewer eggs and fewer recruits in a closed population. Due to different biological processes (density-independence,

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compensation and depensation) affecting S–R dynamics of various species, S–R curves can have a variety of shapes (Hilborn and Walters, 1992). Commonly used S–R models are dome-shaped curves developed by Ricker (1954) and asymptotic curves by Beverton and Holt (1957). The shape of the S–R curve is one of the most important determinants of the capacity of a stock to sustain exploitation and it bears heavily on the appropriate choice of harvest strategy.

Developing S–R relationships for crab stocks is challenging. Due to the fact that crab lack retainable hard body parts that could record growth increments, such as annuli, it is difficult to match parental spawning stocks with their progeny at correct time lags. Further, complex crab reproductive biology and behaviors are not very well understood making it difficult to estimate effective spawning biomass for a given crab stock. Usually, mature biomass of males and females is used as the spawning biomass for a fish stock. A mature male crab usually can successfully mate with more than one mature female and not all mature males contribute to reproductive success (Paul, 1984; Paul et al., 1995; Rondeau and Sainte-Marie, 2001). Due to these difficulties and lack of data, S–R relationships have been estimated for very few crab stocks worldwide. In Alaska, S–R relationships have been developed for only two stocks: Bristol Bay red king crab, *Paralithodes camtschaticus* (Reeves, 1990; Greenberg et al., 1991; Zheng et al., 1995a) and Bristol Bay Tanner crab, *Chionoecetes bairdi* (Zheng and Kruse, 1998).

In this study, we updated the S–R relationships for Bristol Bay red king and Tanner crabs and used results from a length-based model to develop an S–R relationship for eastern Bering Sea snow crab, *Chionoecetes opilio*. First, we developed methods to compute male reproductive potential based on a literature review of red king, Tanner and snow crab reproductive biology. Second, we estimated effective spawning biomass from mature female abundance and male reproductive potential. Finally, we fit effective spawning biomass and recruitment data to both general and autocorrelated Ricker models. We fit other reproductive biomass indices to S–R models for comparison as well. Recruitment was defined as recruitment to the model rather than recruitment to the fishery in this study. We assumed that recruitment consists of crab at

the recruiting age with different sizes and thus indexes year class strength.

2. Methods

2.1. Data

Time series of recruitment and abundance by sex, size and shell condition were derived from the length-based analyses (LBA; Zheng et al., 1995a, 1998) of assessment survey data collected from 1972 to 2001 for Bristol Bay red king crab, from 1975 to 2001 for Bristol Bay Tanner crab and from 1978 to 2000 for eastern Bering Sea snow crab. The recruitment in the first year (1972 and 1975) for red king and Tanner crabs was not estimated in the model. Observed size at maturity and clutch condition data were collected from trawl surveys. The size–weight relationships were $W = 0.022863 CL^{2.2338}$ for red king crab, $W = 0.003661 CW^{2.5639}$ for Tanner crab and $W = 0.000675 CW^{2.9434}$ for snow crab, where W is the weight in grams and CL and CW are the carapace length and carapace width in millimeters (B. Stevens, National Marine Fisheries Service (NMFS), Kodiak, Alaska, pers. commun.).

For Bristol Bay red king crab from 1968 to 1970 and from 1972 to 1974, abundance estimates were obtained from NMFS directly because tow-by-tow survey data are not currently available for these years. All surveys were conducted during summer, except for spring and fall surveys in 1968 and 1969. The average of estimated abundances from spring and fall surveys was used for these 2 years. The abundance in 1971 was derived as the average abundance in 1970 and 1972 because a complete survey was not conducted in 1971. We considered abundance estimates from 1973 to 2000 data to be estimates of absolute abundance; before 1973, estimates were considered as relative abundance because of an apparent change in survey catchability thereafter (Zheng et al., 1995a). These data were used to estimate effective spawning biomass and other reproductive biomass indices from 1968 to 1971.

For Bristol Bay Tanner crab, abundances before 1975 were not estimated by the LBA because electronic data files are not available. However, area-swept estimates of female crab ≥ 80 mm CW from trawl

surveys in 1973 and 1974 and catch per unit effort (CPUE) from the Japanese fleet for large male Tanner crab from 1968 to 1976 are available for the eastern Bering Sea. These data were used to estimate effective spawning biomass and other reproductive biomass indices from 1968 to 1974 (Zheng and Kruse, 1998).

2.2. Time from mating to recruitment

Based on growth data, age of model recruitment of Bristol Bay red king crab was defined as 8 years after mating, corresponding to a mean female CL of 97.4 mm and a mean male CL of 104.2 mm estimated for the year class settling in 1990 (Loher et al., 2001). Male recruitment to the model occurred over a CL range of 95–134 mm with 89.1% within 95–119 mm and female recruitment occurred over a CL range of 90–119 mm with 92.8% within 90–104 mm (Zheng et al., 1995a). The larger CL for male recruits reflects a larger growth increment than females. This time lag is 1 year longer than that based on temperature-dependent growth for Bristol Bay female red king crab (Stevens and Munk, 1990; Zheng et al., 1995a). The year class presumably settling in 1990 (mating in 1989) was much stronger than year classes 4 years before or after it (Fig. 1) and showed very clear modal progression over time (Loher et al., 2001). Time lags of 7 and 9 years were also compared.

For Bristol Bay Tanner crab, female recruitment was distributed over 70–104 mm CW with 97.0% within 70–94 mm CW and a mean of 80.4 mm CW. Male recruitment was distributed over 93–127 mm CW with 92.3% within 93–117 mm CW and a mean of 105.5 mm CW. We estimated that the time from mating to recruitment was 7 years for females and 8 years for males (Zheng and Kruse, 1998). Because male and female recruits have the same trend with a 1-year difference in age, female recruitment in year $t - 1$ was added to male recruitment in year t and a time lag of 8 years was used for total recruitment. For example, females recruited in 1975 were assumed to be from the same cohort as males recruited in 1976. Time lags of 7 and 9 years were also examined for sensitivity of the S–R relationship to this parameter.

Both male and female recruitment of eastern Bering Sea snow crab to the model was assumed to occur primarily within 25–39 mm CW with a mean of 30.4 mm CW. Based on snow crab growth in the Gulf of Saint

Lawrence (Sainte-Marie et al., 1995; Alunno-Bruscia and Sainte-Marie, 1998), time from mating to recruitment for eastern Bering Sea snow crab was assumed to be 4 years. A sensitivity study on time lags of 3 and 5 years was conducted.

2.3. Size at maturity

For Bristol Bay red king and Tanner crabs, sizes at maturity were based on sizes at 50% maturity for females and males. For the purpose of estimating effective spawning biomass, red king crab were assumed to be mature at CL ≥ 120 mm for males and CL ≥ 90 mm for females (Zheng et al., 1995a,b) and Tanner crab to be mature at CW ≥ 113 mm for males and CW ≥ 80 mm for females (Zheng and Kruse, 1998). Due to the fact that mature male and female abundances of eastern Bering Sea snow crab were estimated directly from the LBA, no cut-off size at maturity was assumed for snow crab.

2.4. Computation of effective spawning biomass

2.4.1. Red king crab

We followed Zheng et al. (1995a) to estimate effective spawning biomass for Bristol Bay red king crab. Unlike Tanner and snow crabs, mature female red king crab do not have spermathecae and continue to molt annually. In a laboratory setting, small males (120–139 mm CL) are generally successful at fully fertilizing egg clutches of only 2–3 females (Paul and Paul, 1990) whereas large male crab (>139 mm CL) are generally capable of mating with at least three female crab successfully (Paul and Paul, 1997). Male crab in mating pairs observed in the natural environment are generally much larger in average CL than their female partners (Powell and Nickerson, 1965) and male crab less than 120 mm CL in Kodiak are rarely observed among mating pairs (Powell and Nickerson, 1965). Due to spatial distribution, the number of females with which a male can mate may be less in natural environments than in confined environments. Male reproductive potential is defined as the mature male abundance by CL class multiplied by the maximum number of females with which a male of a particular length can mate (Zheng et al., 1995a). If mature female abundance was less than male reproductive potential, then mature female

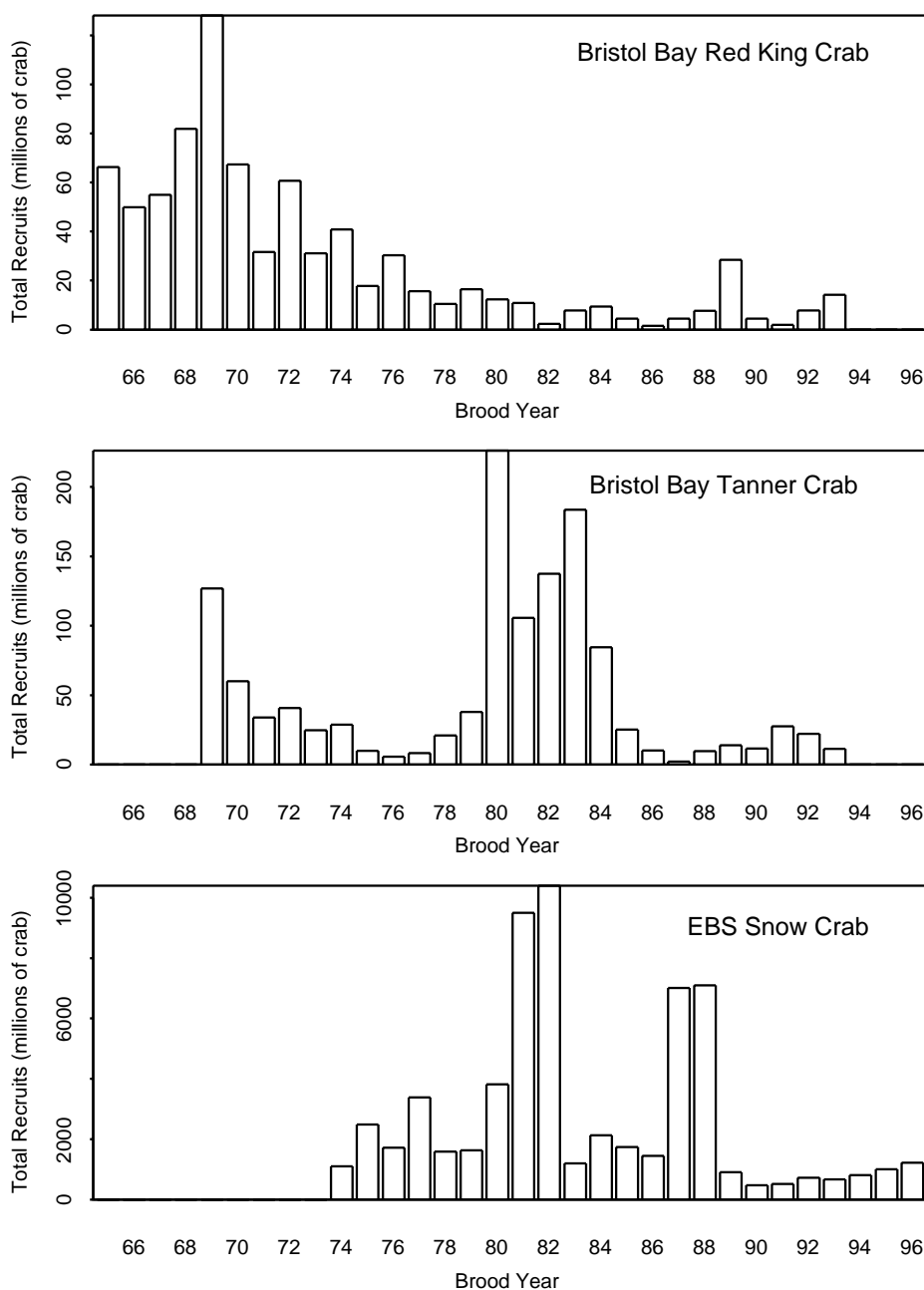


Fig. 1. Total recruits of Bristol Bay red king crab, Bristol Bay Tanner crab and eastern Bering Sea (EBS) snow crab. Time lags from mating to recruiting to the models are 8 years for red king and Tanner crabs and 4 years for snow crab.

abundance was used as female spawning abundance. Otherwise, female spawning abundance was set equal to the male reproductive potential. The female spawning abundance was converted to biomass, defined as

the effective spawning biomass, using the size–weight relationship. We also examined the S–R relationships using total biomass of mature females and total biomass of both mature females and males.

2.4.2. Tanner crab

Computation of effective spawning biomass for Tanner crab is more complex than for red king crab because of its more complex reproductive biology. The average number of females a male can mate with each year depends on molting period duration of the female population, duration of male attendance during mating, population density and male fertilization capability. Following the approach by Zheng and Kruse (1998), annual effective spawning biomass for Bristol Bay Tanner crab, S_t , was estimated as

$$S_t = \sum_l [(NF_{l,t}nr_t + OF_{l,t}or_t)W_l], \quad \iota \geq 80 \text{ mm CW} \quad (1)$$

where $NF_{l,t}$ and $OF_{l,t}$ are the newshell and oldshell female abundances in width class l and year t , W_l the mean weight of female crab in width class l , ι the mid-width of width class l and nr_t and or_t are the ratios of male reproductive potentials TNM_t and TOM_t to newshell and oldshell mature female abundances TNF_t and TOF_t (≥ 80 mm CW) in year t , respectively, that is

$$nr_t = \frac{TNM_t}{TNF_t}, \quad or_t = \max \left[\frac{TOM_{t-1}}{TOF_{t-1}}, \frac{TOM_t}{TOF_t} \right] \quad (2)$$

The male reproductive potentials for newshell and oldshell mature females were defined as

$$\begin{aligned} TNM_t &= \sum_l [(0.3 NM_{l,t} + OM_{l,t})nn_t], \\ 113 \text{ mm} &\leq \iota \leq 137 \text{ mm CW}, \\ TOM_t &= \sum_l [(0.1 NM_{l,t} + OM_{l,t})on_t], \\ \iota &\geq 113 \text{ mm CW} \end{aligned} \quad (3)$$

where $NM_{l,t}$ and $OM_{l,t}$ are the mature male crab abundances in width class l and year t with newshell and oldshell conditions, respectively, and nn_t and on_t are the maximum average number of newshell and oldshell females mated by a matable male (a mature male participating in mating) in year t .

Eq. (2) reflects the fact that female Tanner crab can use stored sperm from multiple matings to fertilize the subsequent 2 years' clutches (Paul, 1984). If nr_t or $or_t > 1$, we set them equal to 1. Based on the influence of male shell condition on mating and the molting duration for primiparous females, we assumed

only 30% of newshell males mate with pubescent or primiparous females and 10% mate with multiparous females (Zheng and Kruse, 1998). We also assumed males < 138 mm CW can mate with both pubescent or primiparous and multiparous females, but males > 137 mm CW mate with only multiparous females because of spatial separation (Zheng and Kruse, 1998). This assumption will slightly affect the mating schedule only in years such as 1987 when an extremely strong recruitment with relatively large sizes at maturity followed several years of poor recruitment. Following Zheng and Kruse (1998), we assumed that a male could mate, on average, with a maximum of five primiparous females and three multiparous females at high mature female density and one primiparous and one multiparous female at low mature female density. Therefore, a male can mate with up to eight females under ideal conditions and two females under the poorest conditions. The maximum average number of females per male at a density between low and high densities was linearly interpolated. The high density was assumed to be the highest estimated density or higher during 1968–2001 and the low density was assumed to be the lowest estimated density during the same period. Like red king crab, we also compared the S–R relationships using total biomass of mature females and total biomass of both mature females and males.

2.4.3. Snow crab

Many similarities exist between the reproductive biology of Tanner and snow crabs, such as storage of sperm by females for future egg fertilization and multiple female mating partners during a given mating season (Paul, 1984; Sainte-Marie and Lovrich, 1994; Sainte-Marie and Carrière, 1995). Like Tanner crab, large oldshell mature males outcompete small newshell males in mating with females (Stevens et al., 1993; Paul et al., 1995; Sainte-Marie et al., 1999). However, male snow crab are sperm conservers, partitioning sperm among successive matings, and female snow crab are polyandrous (Urbani et al., 1998; Rondeau and Sainte-Marie, 2001). Both mate-guarding time by males and the quantity of ejaculate stored in a primiparous female's spermatheca were positively related to the sex ratio of males to females, but these relationships may change over time (Rondeau and Sainte-Marie, 2001). Therefore, lack of males for

mating may rarely occur for snow crab, but sperm limitation can occur naturally if males allocate their sperm too parsimoniously among females (Rondeau and Sainte-Marie, 2001). Because of this sperm economy, it is difficult to use sex ratio to determine effective spawning biomass. Furthermore, depending on temperature, embryo-development of snow crab can take 1 or 2 years (Sainte-Marie, 1993; Moriyasu and Lanteigne, 1998) and we do not have information to separate the abundance of mature females with different embryo-development times annually. In this study, we simply used the sum of total biomass of mature females, morphometrically mature (a differentiation of the shape of chela, i.e., large-clawed, on the basis of the chela height–CW relationship) oldshell males and 30% of morphometrically mature newshell males as effective spawning biomass and examined alternative spawning biomasses, such as total biomass of mature females and total biomass of mature females and morphometrically mature males.

2.5. Stock–recruitment models

Annual recruitment was modeled using a general Ricker curve:

$$R_t = S_{t-k}^{\gamma} e^{\alpha - \beta S_{t-k} + v_t} \quad (4)$$

and an autocorrelated Ricker curve:

$$R_t = S_{t-k} e^{\alpha - \beta S_{t-k} + v_t} \quad (5)$$

where $v_t = \delta_t + \varphi v_{t-1}$, v_t and δ_t are the environmental noises assumed to follow a normal distribution $N(0, \sigma^2)$, k represents the time lag and γ , α , β and φ are the constants. The general Ricker curve describes the density-dependent relationship and the autocorrelated Ricker curve depicts the autocorrelated effects. Eq. (4) was linearized as

$$\ln(R_t) = \alpha + \gamma \ln(S_{t-k}) - \beta S_{t-k} + v_t \quad (6)$$

and Eq. (5) as

$$\ln\left(\frac{R_t}{S_{t-k}}\right) = \alpha - \beta S_{t-k} + v_t \quad (7)$$

An ordinary linear regression was applied to Eq. (6) to estimate model parameters γ , α and β and an autocorrelation regression (procedure AUTOREG, SAS Institute Inc., 1988) by a maximum likelihood method

was used to estimate parameters α , β and φ for Eq. (7). When φ is equal to 0, Eq. (5) becomes an ordinary Ricker model.

3. Results and discussion

Recruitment over time was highly variable for all three crab stocks (Fig. 1). The ratios of the strongest recruitment to the weakest recruitment were 107 for Bristol Bay Tanner crab, 84 for Bristol Bay red king crab and 22 for eastern Bering Sea snow crab. The much higher recruitment levels of snow crab than those of red king and Tanner crabs reflect both the larger snow crab stock and the younger recruitment age in the snow crab model. There was some concurrence of strong and weak year classes among the three stocks (Fig. 1). Strong recruitment occurred from brood years in the late 1960s for both Bristol Bay red king and Tanner crabs and in the early 1980s for both Bristol Bay Tanner and eastern Bering Sea snow crabs. Weak recruitment occurred during the early 1990s for all three stocks. Differences in recruitment patterns include a long-term decline during the 1970s and 1980s for red king crab and strong recruitment of snow crab in the late 1980s (Fig. 1).

The estimated S–R relationships were quite different among the three crab stocks. For Bristol Bay red king crab, strong recruitment generally occurred with intermediate levels of effective spawning biomass and very weak recruitment was associated with extremely low levels of effective spawning biomass (Fig. 2). These features suggest a density-dependent S–R relationship. On the other hand, environmental factors are implicated by strong autocorrelation associated with decadal recruitment; strong year classes occurred in the late 1960s and early 1970s and weak year classes occurred in the 1980s and 1990s. Due to the fact that the autocorrelated curve regards the strong recruitment during the late 1960s and early 1970s as a result of autocorrelation, the recruitment associated with intermediate effective spawning biomass is much lower for the autocorrelated curve than for the general curve (Fig. 2). Likewise, because the autocorrelated curve is less density-dependent, recruitment is much higher than the general curve when effective spawning biomass is very high. Overall, the general Ricker curve fit the data better than the autocorrelated curve

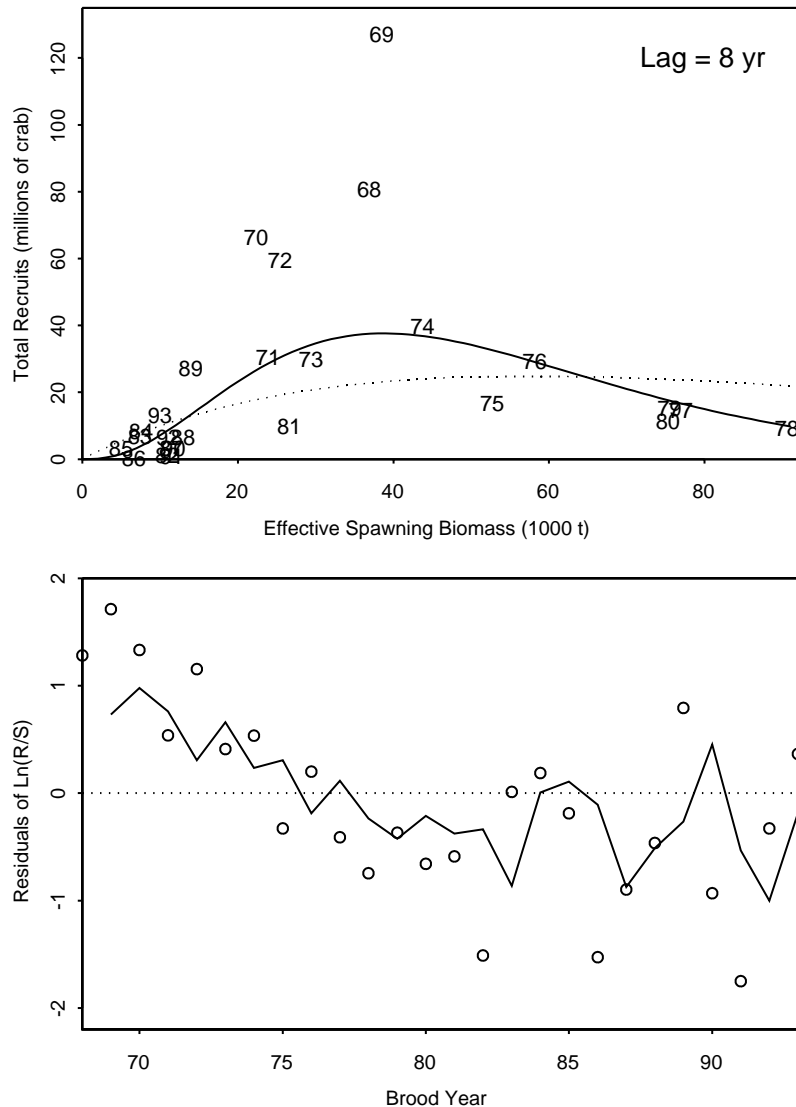


Fig. 2. Relationships between effective spawning biomass and total recruits at age seven (i.e. 8-year time lag; upper plot) and residuals of logarithm of recruits per effective spawning biomass from an autocorrelated Ricker curve (i.e. v_t in Eq. (7); lower plot) for Bristol Bay red king crab. In the upper plot, numerical labels are brood year (year of mating), the solid line is a general Ricker curve and the dotted line is an autocorrelated Ricker curve without v_t values. In the lower plot, the solid line represents autocorrelation estimated from residuals.

(R^2 , Table 1), in contrast to our earlier results when S–R data were fitted up to the 1987 brood year (Zheng et al., 1995a,b). The autocorrelation parameter fit the residuals well only before the 1982 and then fit the residuals poorly (Fig. 2).

Alternative spawning biomass indices fit the S–R models not as well as effective spawning biomass

for Bristol Bay red king crab (Fig. 3). The R^2 for the general Ricker curve were higher with effective spawning biomass (0.567) than with mature female biomass (0.451) and with total mature biomass (0.466) (Table 1). The corresponding R^2 for the autocorrelated Ricker curve are 0.431, 0.346 and 0.368 (Table 1). The fittings with time lags of 7 and 9 years were

Table 1

Parameter estimates of general and autocorrelated (Auto) Ricker stock–recruitment models for Bristol Bay red king crab, Bristol Bay Tanner crab and eastern Bering Sea snow crab with three alternative spawning biomasses (B)

	Effective spawning B						Female B		Total mature B	
	Lag 8		Lag 7		Lag 9		Lag 8		Lag 8	
	General	Auto	General	Auto	General	Auto	General	Auto	General	Auto
Bristol Bay red king crab										
α	−3.600	0.157	−2.585	0.225	−2.861	−0.017	−2.547	0.058	−6.423	−1.120
β	0.070	0.017	0.055	0.018	0.061	0.014	0.049	0.014	0.021	0.005
γ	2.719	NA	2.271	NA	2.358	NA	2.145	NA	2.577	NA
φ	NA	0.571	NA	0.520	NA	0.526	NA	0.505	NA	0.551
d.f.	23	23	24	24	22	22	23	23	23	23
R^2	0.567	0.431	0.446	0.371	0.460	0.398	0.451	0.346	0.466	0.368
Bristol Bay Tanner crab										
α	0.337	1.650	4.126	2.414	−3.331	1.103	1.167	2.135	−0.754	1.387
β	0.128	0.051	0.047	0.079	0.199	0.032	0.112	0.069	0.065	0.034
γ	2.102	NA	0.163	NA	3.919	NA	1.690	NA	1.975	NA
φ	NA	0.697	NA	0.706	NA	0.757	NA	0.666	NA	0.685
d.f.	22	22	22	22	22	22	22	22	22	22
R^2	0.214	0.707	0.239	0.774	0.401	0.689	0.209	0.709	0.177	0.701
	Lag 4		Lag 3		Lag 5		Lag 4		Lag 4	
	General	Auto	General	Auto	General	Auto	General	Auto	General	Auto
Eastern Bering Sea snow crab										
α	13.740	3.477	99.718	2.668	−36.95	4.485	7.179	3.047	60.713	3.433
β	−0.0001	0.006	−0.091	0.002	0.056	0.011	0.002	0.003	−0.026	0.005
γ	−1.176	NA	−20.92	NA	10.563	NA	0.113	NA	−10.70	NA
φ	NA	0.545	NA	0.585	NA	0.444	NA	0.608	NA	0.524
d.f.	16	16	17	17	15	15	16	16	16	16
R^2	0.082	0.466	0.365	0.404	0.339	0.544	0.003	0.453	0.207	0.497

similar, whereas the fitting with a time lag of 8 years was the best (Fig. 4, Table 1). Due to the similar effective spawning biomasses between adjacent years, the shapes of the estimated S–R curves were similar among these three different time lags for either the general Ricker curve or autocorrelated curve.

For Bristol Bay Tanner crab, recruits were not strongly associated with effective spawning biomass; both weak and strong recruitment occurred with both low and high effective spawning biomass (Fig. 5). Strong year classes occurred in brood years from the late 1960s and early 1980s and weak year classes occurred in the mid and late 1970s, mid and late 1980s and early 1990s (Fig. 1); thus, recruitment was highly autocorrelated. As expected, the autocorrelated Ricker curve fit the data much better than the general Ricker curve (Table 1). Much of the variation of recruitment residuals from the ordinary Ricker curve could be

explained by autocorrelation or cycle (Fig. 5). A recruitment cycle of 13 or 14 years was estimated with the S–R data up to the 1989 brood year (Zheng and Kruse, 1998). If this cycle continues, strong recruitment is anticipated for brood years from the mid to late 1990s. Trawl surveys in 2000 and 2001 caught relatively high abundances of crab <60 mm CW (Stevens et al., 2000), which can be a potential indicator of good future recruitment. However, Bristol Bay Tanner crab recruitment is difficult to predict from the abundance of small-sized crab caught in trawl surveys due to their highly contagious distributions. If strong recruitment does not occur soon, the current down cycle will last longer than the previous one.

Alternative spawning biomasses and time lags for Bristol Bay Tanner crab were not very sensitive to the fitting of the S–R models (Figs. 6 and 7; Table 1). For all alternative options considered, the autocorrelated

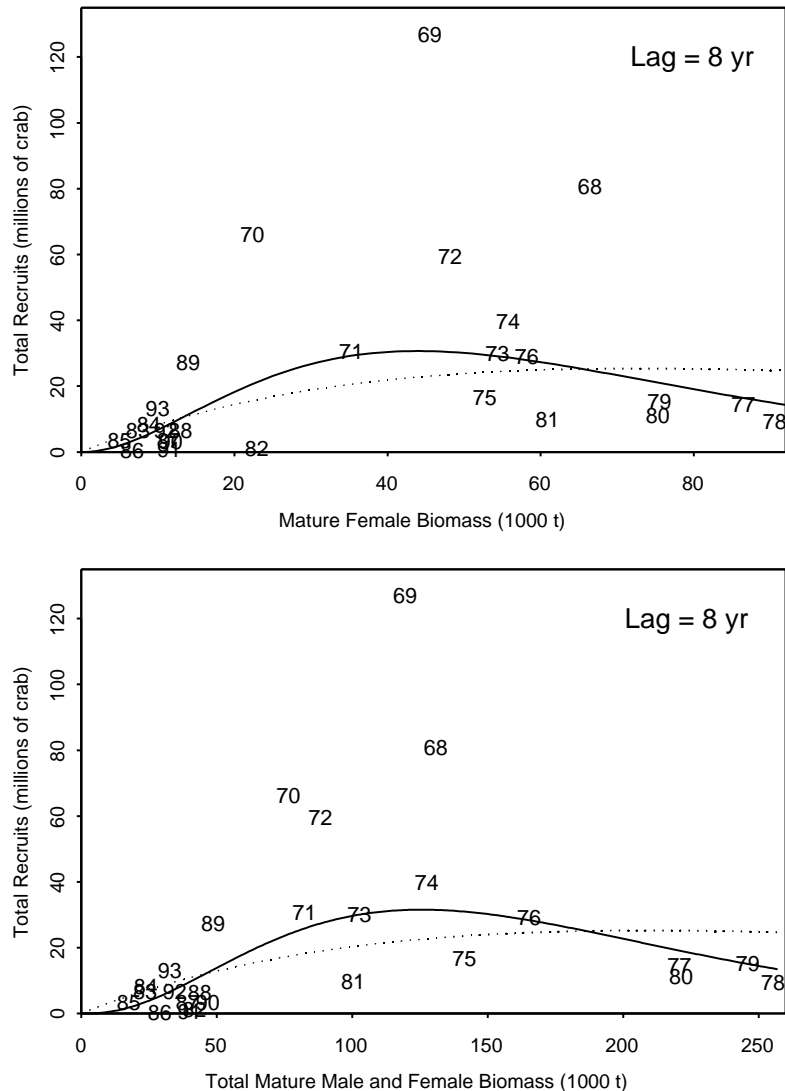


Fig. 3. Relationships between total recruits and mature female biomass (upper plot) and total mature biomass (lower plot) for Bristol Bay red king crab with 8 years of time lag. Numerical labels are brood year (year of mating), the solid line is a general Ricker curve and the dotted line is an autocorrelated Ricker curve without ν_t values of Eq. (5).

Ricker model fit the data much better than the general Ricker curve. The highest R^2 for the general Ricker curve was 0.401 with a time lag of 9 years and the R^2 for the general Ricker curve with the other options were less than 0.24 (Table 1).

The association between recruitment and effective spawning biomass for eastern Bering Sea snow crab was very weak (Fig. 8); effective spawning biomass explained very little recruitment variation with a time

lag of 4 years (Table 1). The S–R relationship indicates a somewhat circular pattern (Figs. 8–10). Like Tanner crab, autocorrelation helps to explain some recruitment variation (Fig. 8, Table 1). The models fit total mature biomass slightly better than effective spawning biomass (Table 1). The fittings of S–R models were sensitive to time lag; the R^2 for the general Ricker curve were much higher with alternative time lags of 3 or 5 years than with a time lag of 4 years

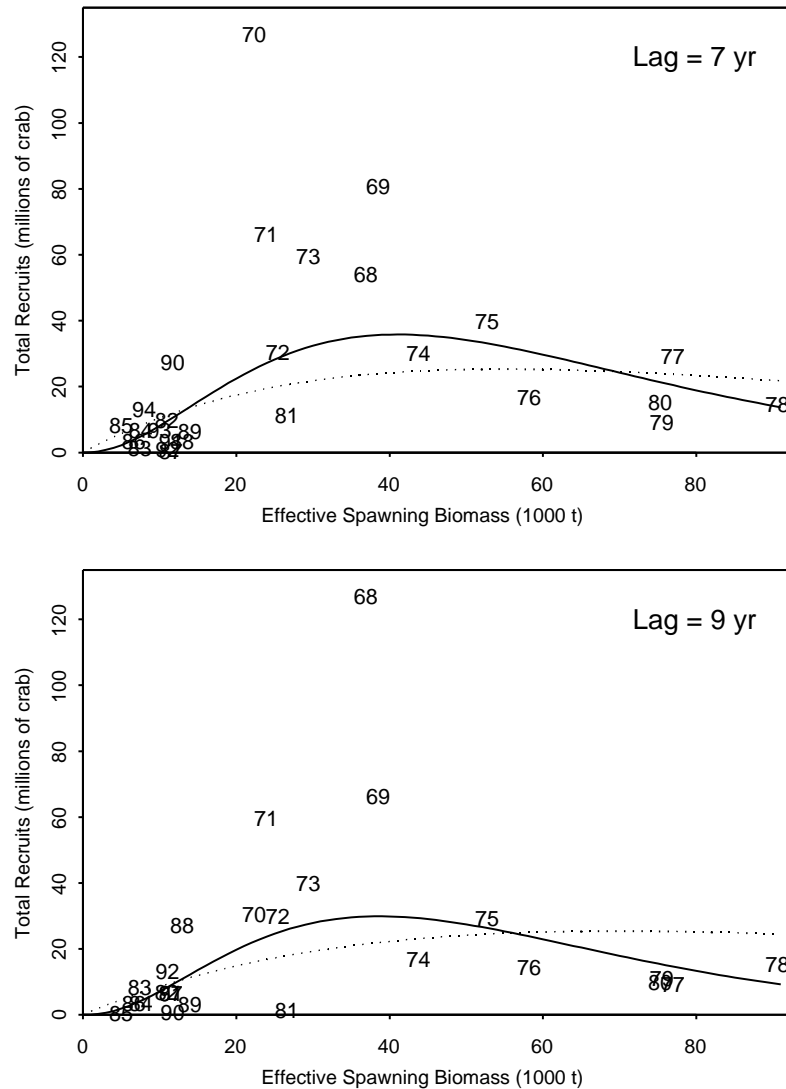


Fig. 4. Relationships between effective spawning biomass and total recruits for Bristol Bay red king crab with 7 years of time lag (upper plot) and 9 years of time lag (lower plot). Numerical labels are brood year (year of mating), the solid line is a general Ricker curve and the dotted line is an autocorrelated Ricker curve without v_t values of Eq. (5).

(Table 1). However, estimated parameters for the general Ricker curves were very unstable among different options (Table 1) and estimated general curves appear to be biologically unrealistic, such as a U-shaped curve with a time lag of 3 years. Therefore, the high R^2 with time lags of 3 and 5 years may be biologically meaningless. The estimated autocorrelated S–R curve with total mature biomass and time lag of 5 years

was more dome-shaped than other estimated curves (Figs. 8–10).

Recruitment patterns and S–R relationships for eastern Bering Sea snow crab were similar to those for snow crab in the Gulf of Saint Lawrence in Atlantic Canada. Periods with strong and weak recruitment alternated every few years, circular patterns of S–R relationships existed and there were very weak

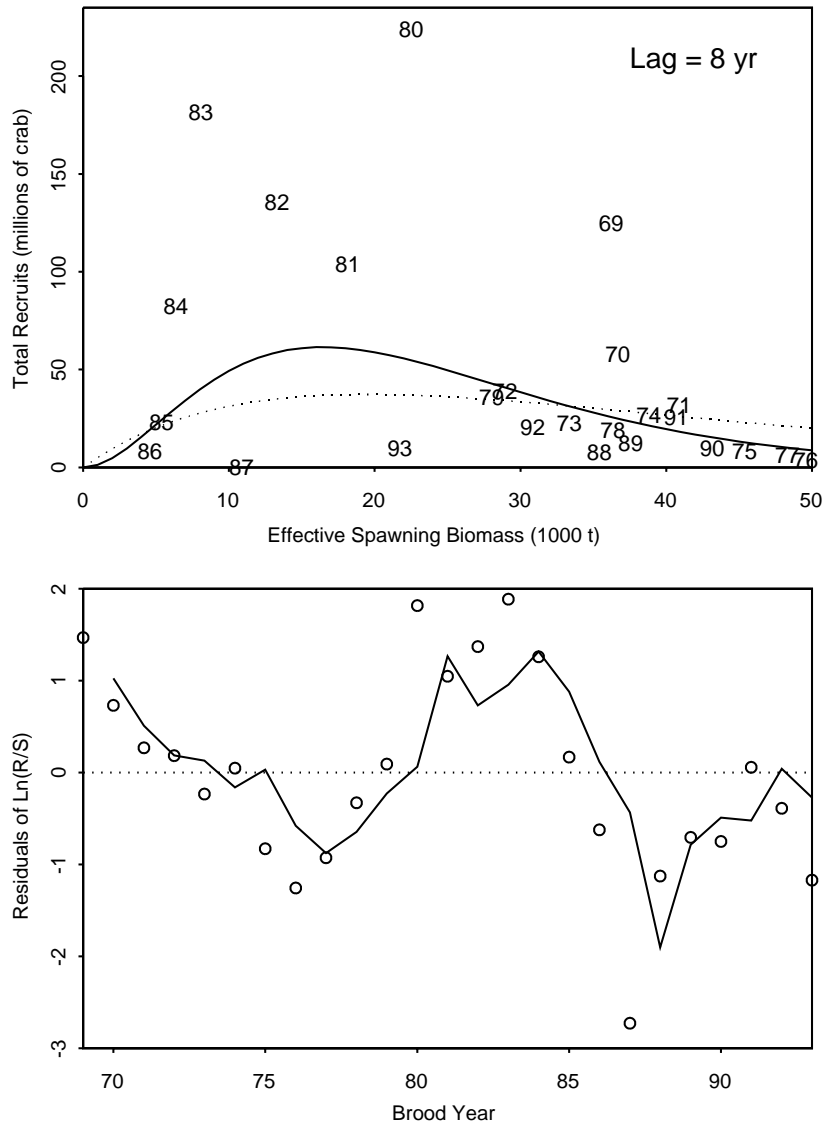


Fig. 5. Relationships between effective spawning biomass and total recruits at age seven (i.e. 8-year time lag; upper plot) and residuals of logarithm of recruits per effective spawning biomass from an autocorrelated Ricker curve (i.e. v_t in Eq. (7); lower plot) for Bristol Bay Tanner crab. In the upper plot, numerical labels are brood year (year of mating), the solid line is a general Ricker curve and the dotted line is an autocorrelated Ricker curve without v_t values. In the lower plot, the solid line represents autocorrelation estimated from residuals.

density-dependent S–R relationships (Sainte-Marie et al., 1996; B. Sainte-Marie, Department of Fisheries and Ocean, Maurice Lamontagne Institute, Canada, pers. commun.). Alternating strong and weak recruitment every few years caused cyclic spawning biomass over time and the time sequence of recruitment and

spawning biomass cycles produced the circular patterns of the S–R relationships.

The S–R relationships were established in a much smaller spatial scale and older recruitment age for Bristol Bay red king and Tanner crabs than for eastern Bering Sea snow crab. This reflects both larger

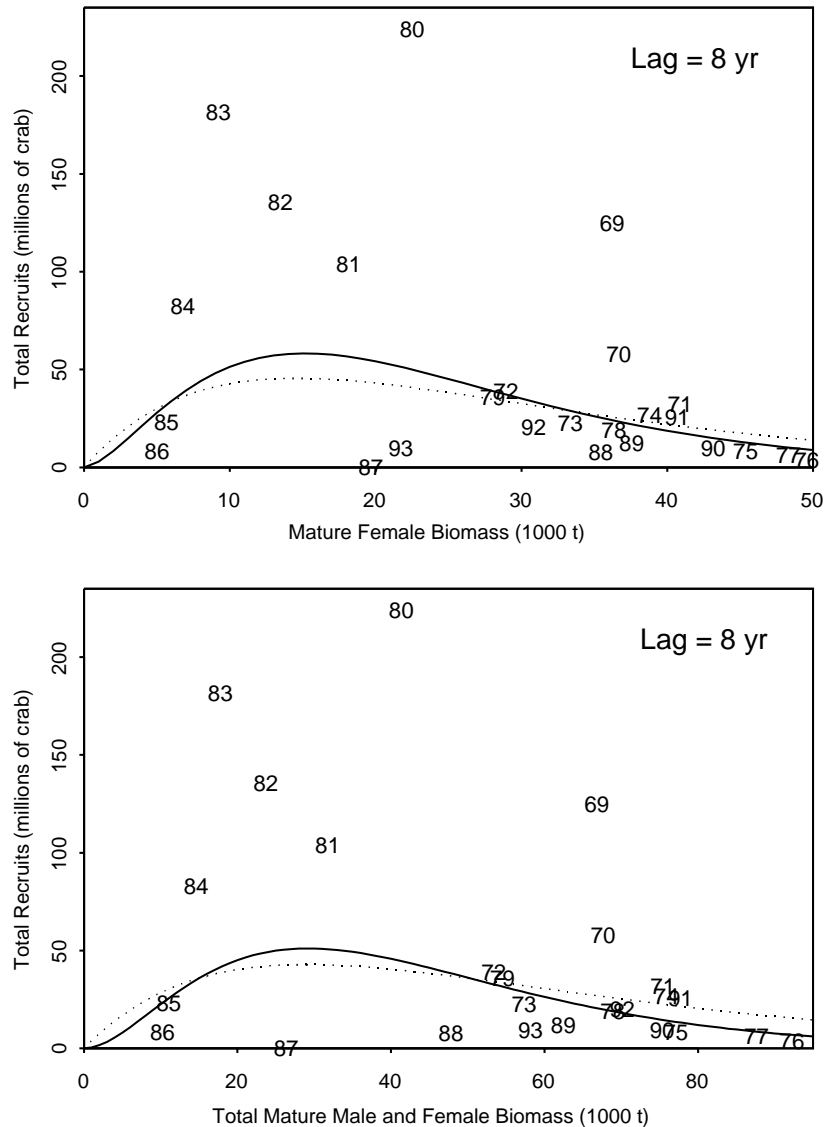


Fig. 6. Relationships between total recruits and mature female biomass (upper plot) and total mature biomass (lower plot) for Bristol Bay Tanner crab with 8 years of time lag. Numerical labels are brood year (year of mating), the solid line is a general Ricker curve and the dotted line is an autocorrelated Ricker curve without v_t values of Eq. (5).

spatial distribution of the snow crab stock and better survey sampling of small snow crab than that of the red king and Tanner crab stocks (Stevens et al., 2000). Red king crab in Bristol Bay consist of a very large proportion of red king crab in the eastern Bering Sea and are generally separate from the small red king crab population off Pribilof Islands (Stevens et al., 2000). In the eastern Bering Sea, Tanner crab are primarily

found in Bristol Bay and the vicinity of the Pribilof Islands (Stevens et al., 2000). The mean CWs at 50% maturity for both male and female Tanner crab generally decrease from east to west and are slightly more than 10 mm larger in Bristol Bay than those of the Pribilof Islands (Somerton, 1981). During the last three decades, about 75% of the commercial catch of Tanner crab in the eastern Bering Sea originated from

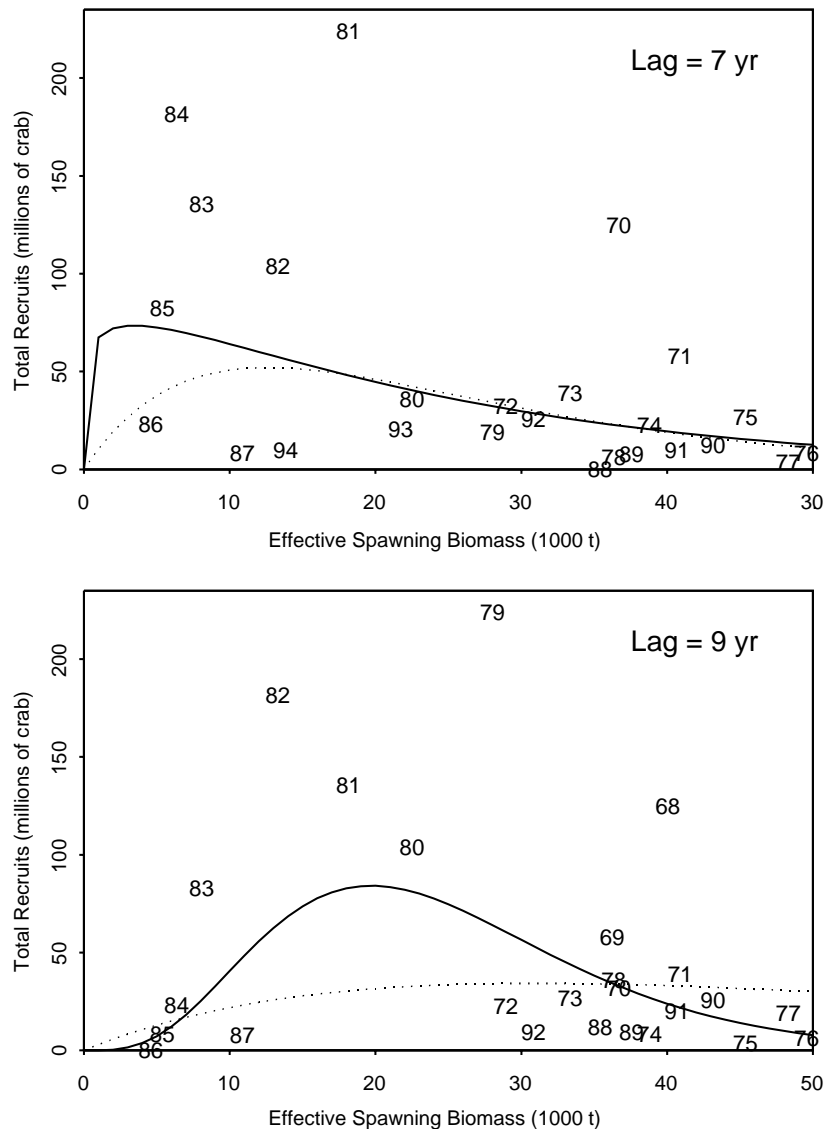


Fig. 7. Relationships between effective spawning biomass and total recruits for Bristol Bay Tanner crab with 7 years of time lag (upper plot) and 9 years of time lag (lower plot). Numerical labels are brood year (year of mating), the solid line is a general Ricker curve and the dotted line is an autocorrelated Ricker curve without v_t values of Eq. (5).

the Bristol Bay area. There may be some immigration and emigration of Tanner crab between Bristol Bay and the vicinity of the Pribilof Islands. However, because the recruitment and abundance trends of Tanner crab in these two areas were similar, the impact of this immigration and emigration or larvae importation on estimated S–R relationships may be small.

Older recruitment ages may reduce survey measurement errors of the stock assessment but increase aging errors for recruitment, which can affect estimated S–R relationships and increase autocorrelation among estimated recruitments. Temperature-dependent growth of juvenile crab (Stevens, 1990) may further increase aging errors of recruitment estimated by a length-based

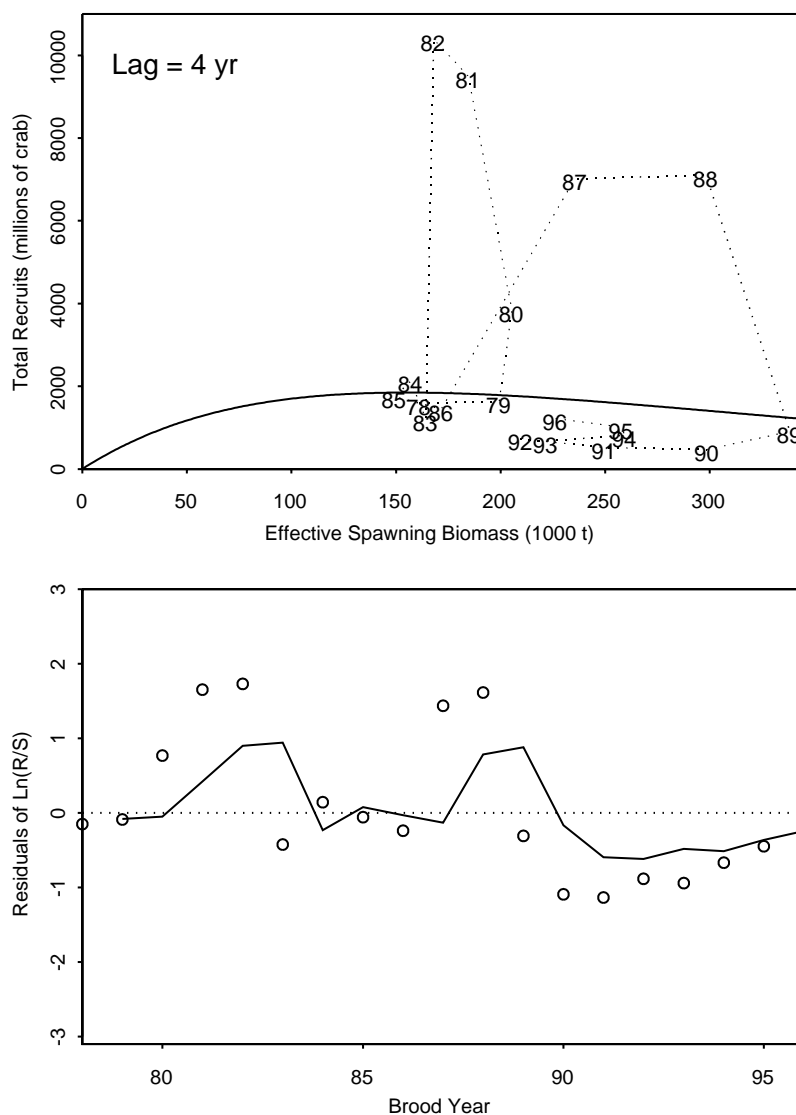


Fig. 8. Relationships between effective spawning biomass and total recruits at age three (i.e. 4-year time lag; upper plot) and residuals of logarithm of recruits per effective spawning biomass from an autocorrelated Ricker curve (i.e. v_t in Eq. (7); lower plot) for eastern Bering Sea snow crab. In the upper plot, numerical labels linked by the dotted line are brood year (year of mating) and the solid line is an autocorrelated Ricker curve without v_t values. In the lower plot, the solid line represents autocorrelation estimated from residuals.

model. Without accurate aging techniques, aging errors are always a problem for developing crab S–R relationships. However, the modal progressions, when they existed, were modeled well in the length-based models (Zheng et al., 1995a,b, 1998) and the model estimated recruitment for the most distinctive year class of red king crab in Bristol Bay in three decades,

the 1989 year class, appears to index the year class strength very well. Also, because of relatively weak density-dependent S–R relationships for these three crab stocks, increasing or decreasing time lag by 1 year generally does not affect the estimated S–R relationships greatly. Overall, the impacts of aging errors on estimated crab S–R relationships are difficult to

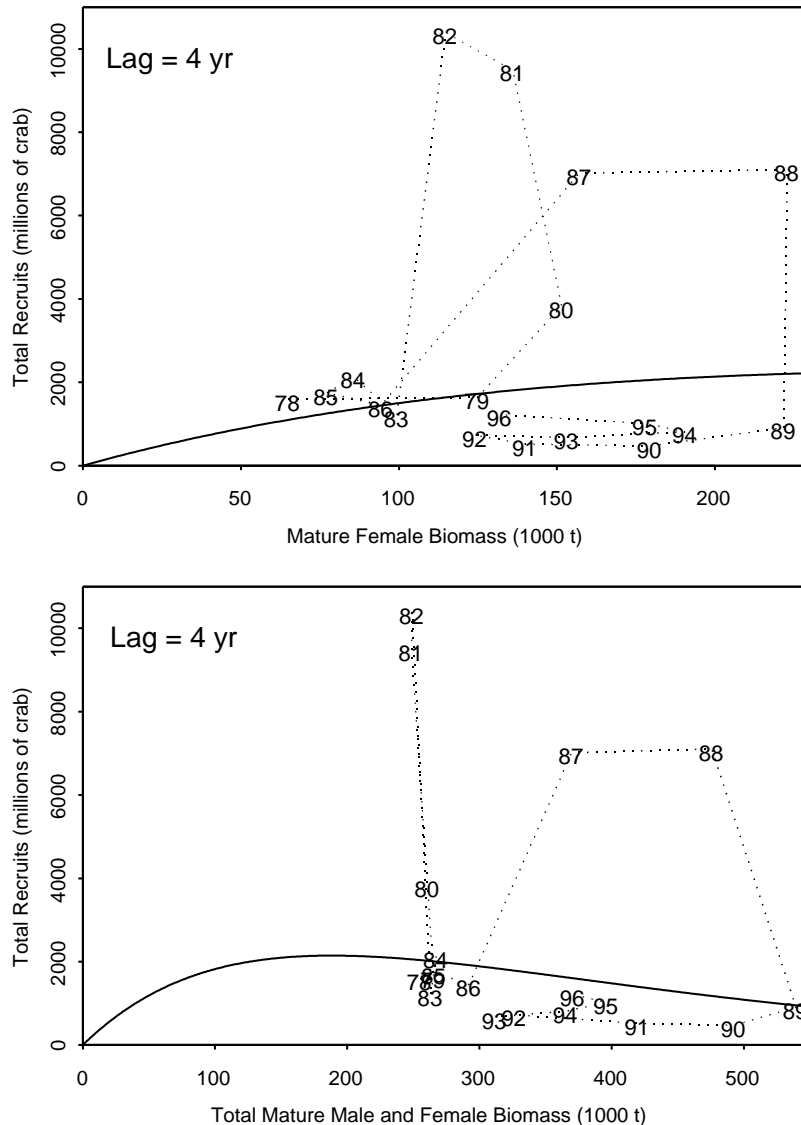


Fig. 9. Relationships between total recruits and mature female biomass (upper plot) and total mature biomass (lower plot) for eastern Bering Sea snow crab with 4 years of time lag. Numerical labels linked by the dotted line are brood year (year of mating) and the solid line is an autocorrelated Ricker curve without v_t values of Eq. (5).

quantify and the aging errors can greatly be reduced only with the future development of an accurate aging technique.

Strong autocorrelation of recruitment time series and periodic or quasiperiodic behavior of recruitment are common in many crab stocks and some fish stocks. Besides these three crab stocks, recruitment is autocorrelated for other crab stocks in Alaska as well (Zheng

and Kruse, 2000). Recruitment to red king crab stocks in the northern Gulf of Alaska and along the Aleutian Islands was strong during the late 1970s and has been weak since the mid-1980s. Recruitment to eastern Bering Sea blue king crab *Paralithodes platypus* stocks was strong in the mid and late 1970s, weak in the mid-1980s and relatively strong in the 1990s. Recruitment to Tanner crab stocks in the northern Gulf

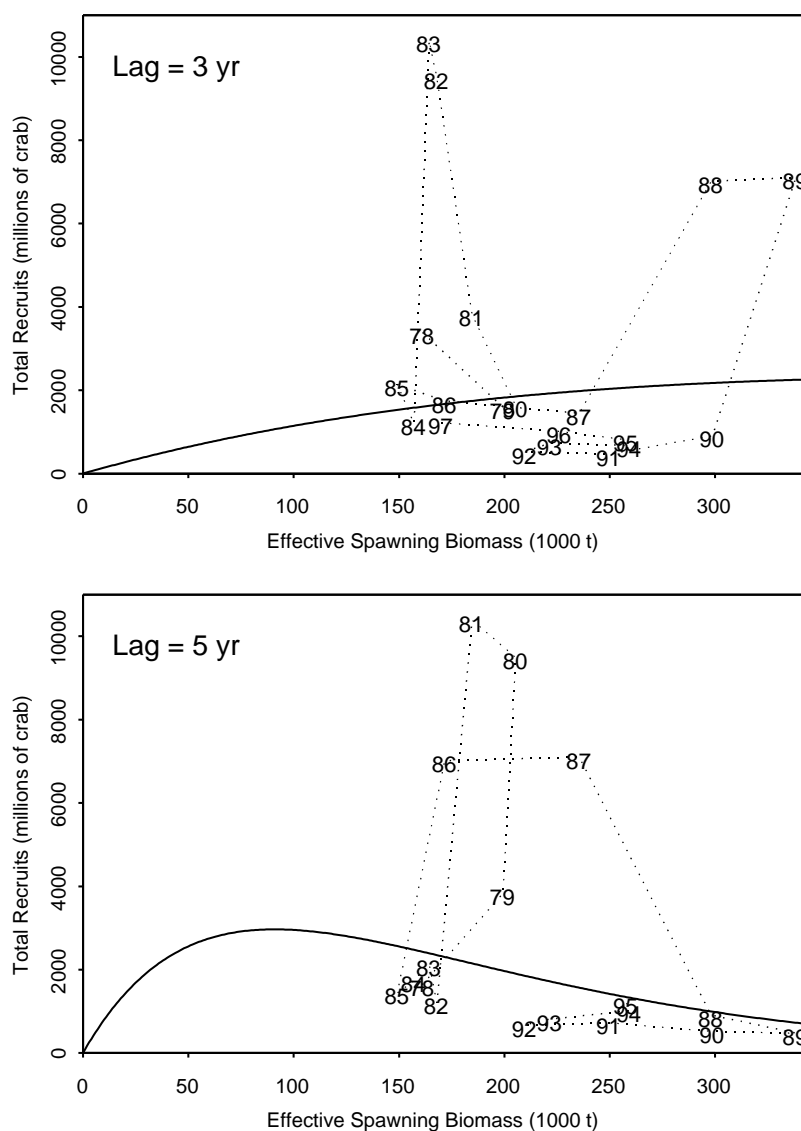


Fig. 10. Relationships between effective spawning biomass and total recruits for eastern Bering Sea snow crab with 3 years of time lag (upper plot) and 5 years of time lag (lower plot). Numerical labels linked by the dotted line are brood year (year of mating) and the solid line is an autocorrelated Ricker curve without v_t values of Eq. (5).

of Alaska was strong in the mid-1970s and has been weak since the early 1990s. Recruitment of many fish stocks has periodicities ranging from 10 to 26 years (Koslow, 1989).

The causes for crab recruitment cycles are unknown. There is evidence that some stocks were overfished in some years, but crab population dynamics are complex and cannot be explained by fishing mortality alone

(Kruse et al., 1996). Large variance in brood strength from similar spawning stock sizes and autocorrelated recruitment time series imply that environmental factors are likely to play a very important role in year class formation.

The dynamics of the coupled ocean–atmosphere system of the North Pacific is composed of several important time scales of variability including El Niño

events that occur every 3–7 years and decadal-scale regime shifts, largely attributed to shifts in the Aleutian Low and other atmospheric pressure systems in winter (Niebauer, 1988; Trenberth and Hurrell, 1994). Associated changes in ocean circulation, sea level, temperature, salinity and mixed layer depth have significant effects on primary and secondary productivity and recruitment of fish stocks (Brodeur and Ware, 1992; Hollowed and Wooster, 1992; Beamish and Bouillon, 1993). Likewise, recruitment trends to many Alaskan crab stocks may be related to decadal climate shifts (Zheng and Kruse, 2000), but leading cause and effect mechanisms may be species specific.

Many Alaskan red king crab stocks, including Bristol Bay, tend to have periods of weak recruitment that coincide with decades of strong winter Aleutian Lows, the opposite of trends for many fish stocks (Hollowed and Wooster, 1992; Beamish and Bouillon, 1993). The mechanisms are uncertain, but food availability is hypothesized to be important to red king crab (Zheng and Kruse, 2000) because their larvae suffer reduced survival and feeding capability if they do not feed within the first 2–6 days after hatching (Paul and Paul, 1980). Diatoms such as *Thalassiosira* are important food for first-feeding red king crab larvae (Paul et al., 1989) and they predominate the spring bloom in years of light winds when the water column is stable (Ziemann et al., 1991; Bientang and Ziemann, 1995). One hypothesis is that years of strong wind mixing associated with intensified Aleutian Lows may depress red king crab larval survival and subsequent recruitment (Zheng and Kruse, 2000).

Differences in life histories and recruitment trends suggest that the processes regulating Tanner crab recruitment may differ from those of red king crab (Tyler and Kruse, 1998). Statistical evidence exists for the following recruitment processes for eastern Bering Sea Tanner crab: (1) colder than average bottom temperatures adversely affect egg development; (2) winds from the northeast along the north side of the Alaska Peninsula promote coastal upwelling while advecting larvae offshore to nursery areas of fine sediments; (3) warm sea surface temperatures promote increases in *Pseudocalanus* copepod nauplii, the primary prey of Tanner crab larvae (Rosenkranz et al., 1998, 2001).

Exploratory analyses of recruitment mechanisms for eastern Bering Sea snow crab have not begun. In the Northwest Atlantic, Sainte-Marie et al. (1996) hy-

pothesized that density-dependent mortality in juvenile nurseries may cause alternating periods of strong and weak recruitment for snow crab. A strong crab cohort may colonize and saturate available nurseries such that settling megalopae from subsequent cohorts are cannibalized by larger immature crab or are forced to use suboptimal habitats, which may lower survival rates (Sainte-Marie et al., 1996). Once the resident cohort achieves sexual maturity, they move offshore to join the reproductive population, thus vacating the nursery areas for recolonization by a subsequent year class. While this hypothesis has not been proven, it is intriguing as it may help to explain the apparent circular S–R pattern for snow crab in the eastern Bering Sea and Northwest Atlantic. On the other hand, Dawe et al. (1997) suggested that temperature directly affected year class strength of snow crab in the Newfoundland region.

These and alternative environment–recruitment hypotheses for Alaskan crab stocks have yet to be thoroughly investigated. Major changes in groundfish abundance have prompted crab recruitment hypotheses involving interspecific relationships, such as groundfish predation and competition (Kruse and Zheng, 1999). These alternatives warrant closer examination through computer simulation modeling and field and laboratory studies.

Even if the S–R relationship has not been clearly demonstrated for each stock and species, it is prudent to assume an effect of stock size on recruitment, at least at low reproductive stock levels, to avoid risk of commercial extinction. Most crab stocks in the Gulf of Alaska have been depressed for 2–3 decades with few signs of recovery. Stock may affect recruitment differently than we modeled. For instance, spawning geography (i.e. the spatial distribution of spawners) is one possible confounding effect of stock on S–R relationships that has not been explicitly considered to date.

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